ON THE VASCULAR ANATOMY OF THE CYCADEOID CONE AXIS1

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The great fossil cycad beds of the Black Hills in South Dakota and the Freezeout Hills of Wyoming have yielded a tremendously valuable store of knowledge concerning the internal structure of this early and highly specialized group of plants. Nevertheless, a considerable number of questions remain unanswered concerning the Cycadeoids themselves as well as their affinities with other groups. Some of this information will be obtained from further study of the specimens that have long reposed in American museums, and it is hoped that discoveries of new localities will play a still more important part.

It is the purpose of the present contribution to record a fossil cycad locality in the Ferris Mountains of south-central Wyoming and to describe certain imperfectly known features of the vascular anatomy of the Cycadeoidea cone axis.

In 1941, when I was collecting fossils in Wyoming, the Ferris Mountain locality was brought to my attention by Mr. W. A. Brox, a geologist and mineral dealer of Rawlins. He showed me a number of silicified cycad fragments in his collection which had been found in those mountains by Mr. Charles Johnson, of Bairoil. Through the generous aid of these two gentlemen a visit to the site was made possible. Only a few supplementary fragments were obtained at that time but these were sufficient to indicate the origin of the specimens. The locality, which was discovered by Mr. Johnson, lies near the west end of the Ferris Mountain range, approximately 10 miles northeast of Bairoil, Wyoming. The fossils had apparently weathered out of the upper Jurassic Morrison formation, in all probability occupying the same or nearly the same horizon as the fossil cycads from the Freezeout Hills, some 50 miles to the east.

Of the specimens obtained from Mr. Brox and from Mr. Johnson, one consists of the apical portion of a columnar trunk. Prior to sectioning for study it was 12.5 cm. long and nearly 15 cm. in diameter. That it is the tip of a trunk or branch is clearly indicated by the rapidly tapering form of the xylary "cylinder" and the dense aggregation of the leaf bases composing the upper surface. The trunk fragment was cut transversely into four sections, and while a study of the exposed surfaces revealed no exceptional features not already known in Cycadeoidean anatomy a number of cone axes was noted. In view of the excellent preservation and the highly gratifying quality of the peels obtained it seemed probable that serial preparations would reveal significant information pertaining to the stem-peduncle xylem transition.

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General Anatomy .-

As is usual in the genus Cycadeoidea, the pith is large, measuring 4 cm. in diameter, and it is liberally supplied with irregular, and probably secretory, sacs. These are found both in the cortex and leaf bases and are also filled with a dense brown substance throughout.

The stele consists of a cylinder 6-8 mm. thick (radially) which is frequently segmented by the departure of leaf and cone traces. Xylem and phloem are present in approximately equal quantities and are readily distinguished in transverse and radial sections. The tracheids are predominantly scalariform (fig. 9), and there is no evidence of distinct annular growth in transverse section, the wood presenting the aspect of a single uniform ring.

Where the xylem is undisturbed by departing appendage traces the wood rays are generally uniseriate and of considerable height. A few have been observed only 3–4 cells high but the majority are 15 or more cells high. Not infrequently they tend to be biseriate in the central portion. The ray cell size is very variable, ranging from 105 μ high by 48 μ broad (tangential) to 24 μ x 12 μ .

The Stem-Peduncle Stele Transition .-

In Wieland's monumental treatment² of the American petrified cycadean trunks he gives an account of the anatomy of the lower portion of the peduncle stele of Cycadeoidea Wielandi Ward. The equipment available at the time rendered impossible the preparation of serial sections, and it is to Wieland's credit that he was able to shed as much light on the stem-peduncle stele transition as he did. However, as he indicates in his summary (p. 73), the description that he was able to present is incomplete and difficult to follow. In view of the seemingly significant and distinctive nature of the peduncle anatomy it seems appropriate to quote his summary:

The general conclusion is that the peduncular bundle is formed from the union of several different bundle strands in the lower part of its course through the cortex, and that these strands consist primarily of a main branch arising directly from the woody cylinder, which may, however, be connected with either lateral or subtending leaf traces. The leaf traces appear in general to arise from the woody cylinder as horseshoe bundles, with the phloem outside, these bundles soon assuming a more or less brokenly-circular form in the most of their course through the cortex before dividing up in the leaf base.

As a generality, this summary is quite correct although there are many gaps in the description which render it, according to Wieland himself, "unexpected difficult to explain." In the following paragraphs I shall present a detailed account of the stelar anatomy of the peduncle from its origin in the stem stele to its departure from the trunk as a free appendage.

In following the transition from below upwards the first indication of the departure of a peduncle stelar system presents itself in the form of three arcs of xylem about 4 mm. apart (fig. 1). Of these, the two laterals (a, b), which are markedly more elongate radially than ordinary leaf traces, depart rather abruptly from the stele while the central trace (c), as may be noted in the succeeding photographs, passes out into the cortex much more slowly.

² Wieland, G. R. American fossil cycads. Carnegie Inst. Washington Publ. 34¹. 1906.

Soon after their departure from the stem stele each of the two lateral traces closes to form a radially elongate stele. Almost immediately these become centrally constricted, foreshadowing their rapid division into two more or less equal parts. In fig. 2 it is clear that the two pairs of arcs, a_1 , a_2 and b_1 , b_2 , have resulted from the respective divisions of a and b in fig. 1. The preservation in the region of the b lateral is rather faulty, which accounts for the light streak through the photograph. Aside, however, from some slight size differences, the system is bilaterally symmetrical and consequently we may center the discussion around the more perfectly preserved a lateral.

Next the a_2 and b_2 segments of the two laterals pass directly out, each into a petiole base. The further division of these traces in the petioles involves no features that are not already known in Cycadean anatomy and need not be considered further. Now the inner segments of the laterals (a_1, b_1) close in, resulting in two nearly cylindrical steles. These pass to a position closely flanking the now radially extended central trace (fig. 3), open directly toward it, and the three fuse, resulting in a short cross-shaped figure (fig. 4)³. This appendage system, which is still connected with the stem stele, is then pinched off (fig. 5) from the latter and tends to take the shape of an ellipse. One more departure is, however, in the order of things. The outer portion (c_1) of the original central trace c passes out (fig. 6) into a petiole which directly subtends the peduncle. The stele of the latter then departs from the cortex without further additions or losses. The entire transition from fig. 1 to fig. 6 extends through a vertical distance of 12 mm.

A number of other peduncle steles have been followed through parts of their lower course, sufficient to establish the above description as typical. It seems very likely, moreover, from a comparison with Wieland's figures⁴ that essentially the same structural relationships prevail in Cycadeoidea Wielandi Ward. Beyond this, a generalization is speculative but in view of the rather close comparison in other anatomical details between C. Wielandi and my own specimen with numerous other species of Cycadeoidea it seems safe to predict that the transition described here will be found to be typical for most of the closely related species.

Taxonomy .-

If one looks at all carefully into the literature relating to petrified cycadean stems it soon becomes clear that a majority of the specific names are quite meaningless as biologic entities. It seems to have become standard practice to assign a new specific name to each newly discovered specimen. However, it is not as difficult as might be expected to condone this custom despite the abundance of names that results. The fact remains that one rarely encounters paleobotanical specimens that present greater difficulty in their preparation of study material.

One of the initial saw cuts was made near that portion of the block shown in fig. 4. Thus in order to survey the course of the peduncle stele it was necessary to prepare peels from both of the adjoining surfaces. Consequently figs. 4, 5, and 6 are reversed, lateral b appearing at the left instead of the right as in the preceding fig. 3. It seemed best to illustrate the series this way since somewhat inferior prints were obtained when the negatives of either half of the series were reversed.

⁴ Wieland, op. cit. pp. 69-71.

This, coupled with the hesitancy on the part of many investigators to dissect specimens of museum-display quality, has resulted in the description of a great many specimens concerning which little or nothing of importance is known. Ward's descriptions, based almost exclusively on external characters, are very nearly worthless. Until the internal structure of those species is investigated the names remain only as catalogue numbers. Even in Wieland's informative and beautifully executed volumes I personally find it difficult to single out distinctive characters for very many of the numerous species that are recorded.

This is perhaps a weak excuse to carry on a weak and incomplete system. Nevertheless, the Cycadeoid described here might be "tentatively assigned" to a number of recorded species, one, all or none of which choices might be correct. In view of this uncertainty it seems that less ultimate confusion will arise if it is recorded, for the present, as a distinct taxonomic entity.

Cycadeoidea Broxiana Andrews, n. sp.

Species based on the apical portion of a columnar type trunk; pith 4 cm. in diameter, containing abundant secretory sacs, the latter also found in cortex and petioles; stele a single cylinder 6–8 mm. thick, xylem and phloem quantitatively equal, tracheids scalariform, rays uniseriate, occasionally biseriate, cells very variable in size; ramentum abundant about bases of petioles and peduncles; leaf trace branches about 20, ventral ones turned strongly inward; periderm well developed in cortex of peduncle and peduncular bracts. Type specimen (#1463) deposited in the collections of the Henry Shaw School of Botany, Washington University, St. Louis.

Acknowledgment .-

I wish to express my sincere appreciation to Mr. W. A. Brox, of Rawlins, Wyoming, for valuable aid in the field and his unselfish gift of botanical specimens of scientific value.

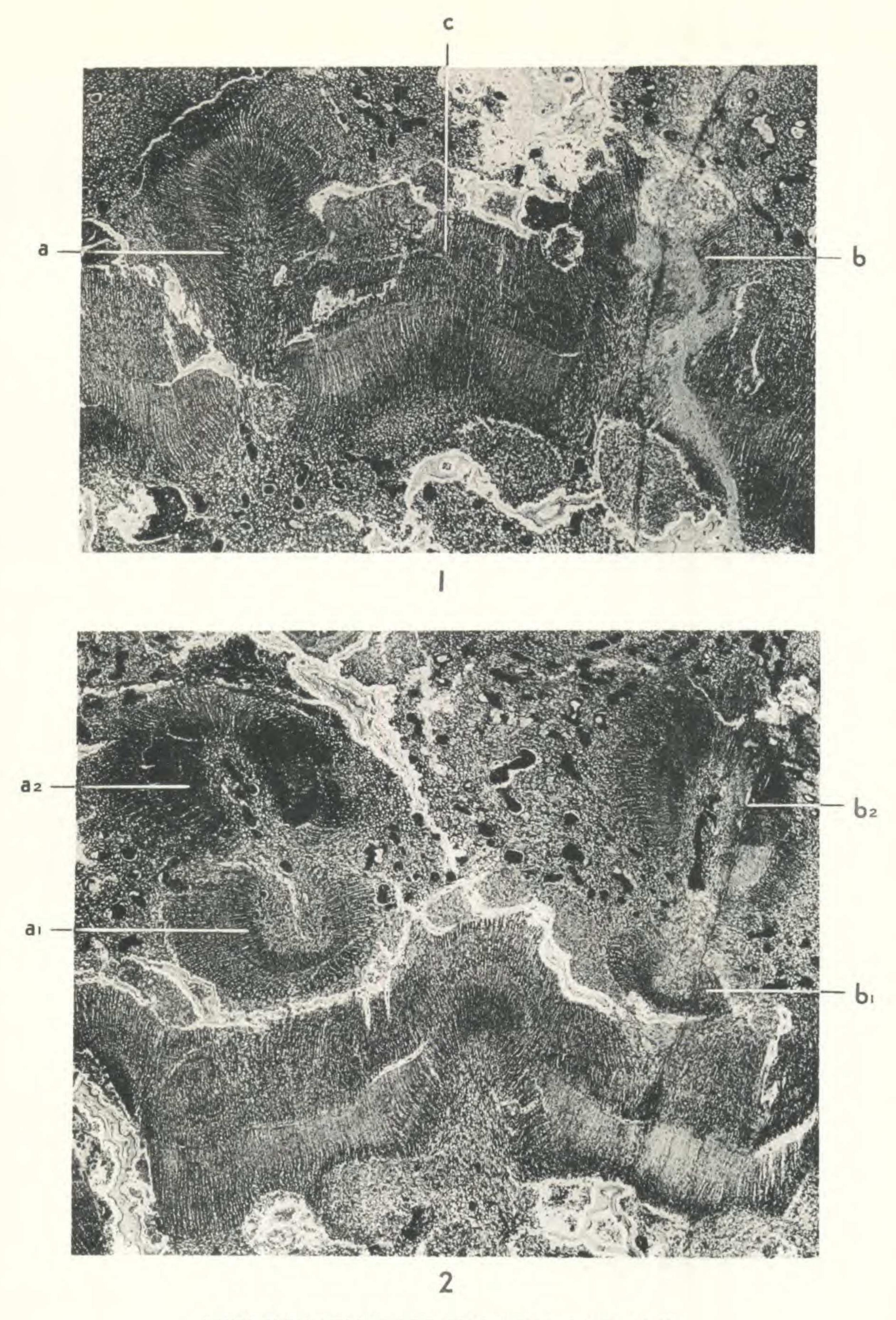
EXPLANATION OF PLATE

PLATE 6

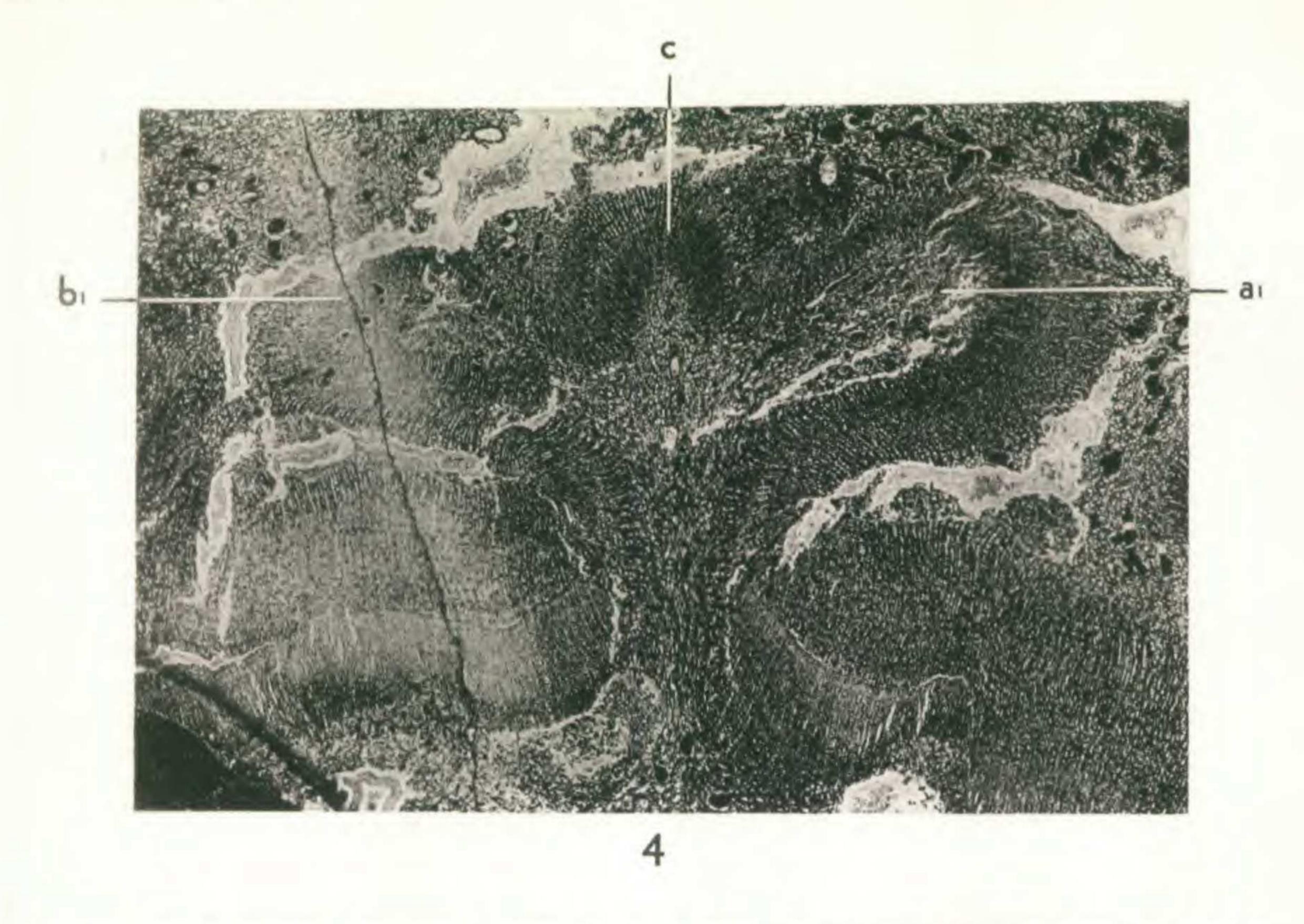
Cycadeoidea Broxiana

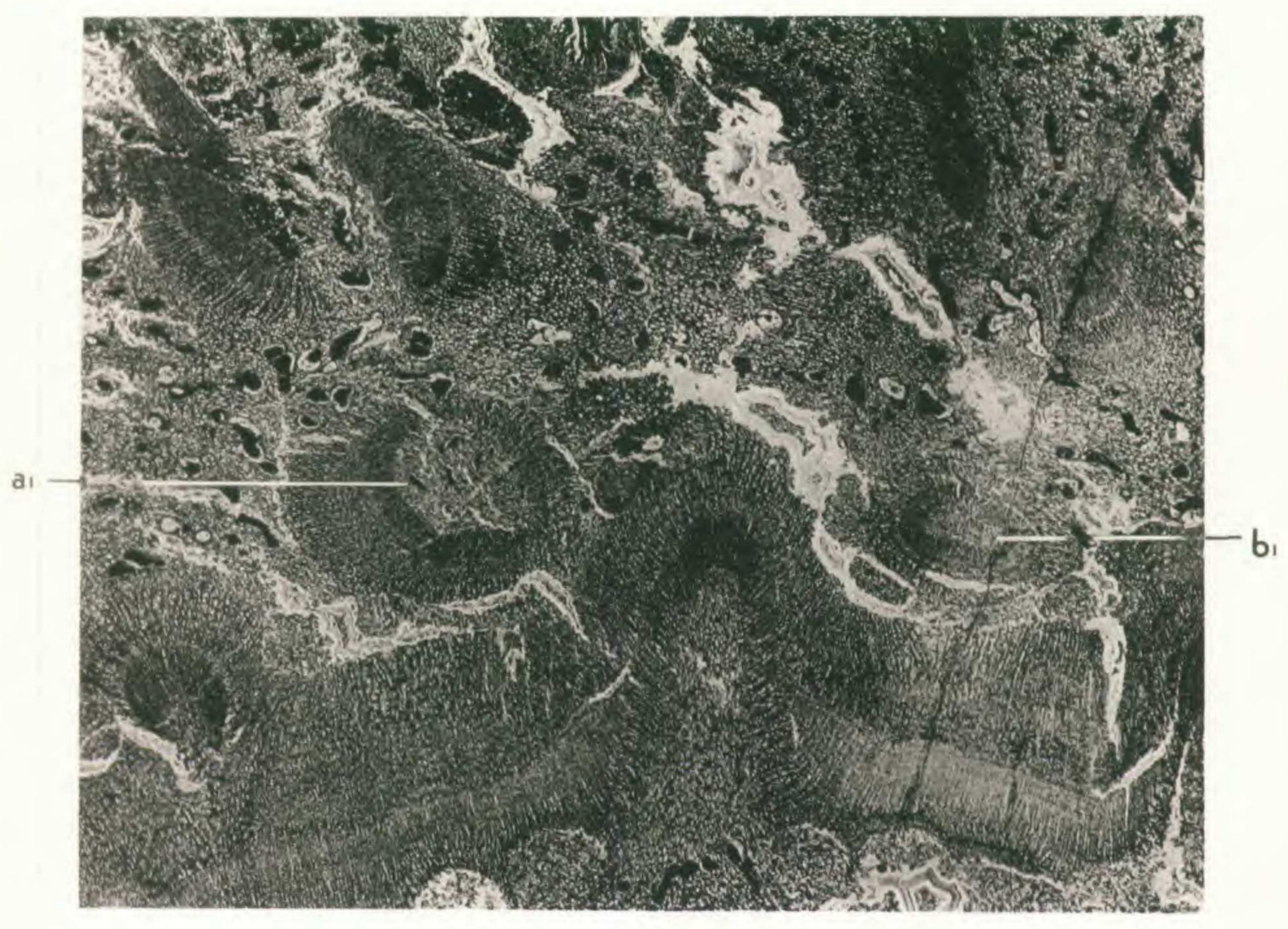
Fig. 1. Transverse section through stem stele showing origin of peduncular traces; a, b, lateral traces, and c central trace. 1463C-a, t27; x 5.

Fig. 2. Same at a higher level showing division of the lateral traces. The traces, a_1 , a_2 and b_1 , b_2 have resulted from the tangential divisions of a and b (fig. 1) respectively. 1463C-a, t17; x 5.



ANDREWS-THE CYCADEOID CONE AXIS





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EXPLANATION OF PLATE

PLATE 7

Cycadeoidea Broxiana

- Fig. 3. The laterals a₁ and b₂ have closed and are about to fuse with the now elongated central trace. 1463C-a, t8; x 5.
 - Fig. 4. Showing fused lateral and central traces. 1463B-B1; x 5.